CONTRIBUTIONS TO PALÆONTOLOGY

I

NEW MERYCODONTS FROM THE UPPER MIOCENE OF NEVADA

By Eustace L. Furlong

With five plates

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CONTENTS

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INTRODUCTION

In an Upper Miocene assemblage of mammals recently brought together, occur remains of numerous individuals referable to the genus *Merycodus*. The collection represents several seasons of palæontological field work by parties from the California Institute of Technology in the vicinity of Tonopah, Nevada.

The specimens of *Merycodus* exhibit characters that are not common to those of species described from other localities in the Great Basin Province or from West Coast Miocene and Pliocene deposits. In some respects, the new Nevada forms combine characters seen in *M. furcatus* and *M. necatus*, found in deposits of similar age. Differences of structure among the materials represented indicate the presence of two distinct species of Tonopah merycodonts.

In a study of the new types, an analysis of the morphologic characters of the genus emphasizes the essentially constant premolar tooth pattern for *Merycodus*. As may be expected, greater diversity occurs among merycodont horn-core structures, particularly as to shape and size. However, the supraorbital position of the horn-cores is apparently constant within specific groups.

In the present comparative studies, I am particularly indebted to Dr. Charles L. Camp and to Mr. R. A. Stirton of the Museum of Palæontology, University of California, for the loan of *Merycodus* material. Mr. John L. Ridgway has prepared the drawings and has arranged the plates.

OCCURRENCE

Remains of *Merycodus* from near Tonopah were found associated with *Merychippus*, *Hypohippus*, Rhinoceros, Camel, *Pseudælurus* and other Miocene mammals at California Institute Technology Locality 172. The bone bed occurred in a relatively restricted area in the San Antonio Mountains and in strata referred to Esmeralda Miocene.

The matrix surrounding the bone is a fine clay to a coarse, pebbly sandstone and occasionally a siliceous chert. Some of the fossil bones were imbedded in part in the softer matrix and in part in the indurated chert. Lenses of the latter in the deposit suggest that deposition occurred in a small lake or in ponds.

PRESERVATION AND DESCRIPTION OF MATERIAL

No complete skulls or mandibles of *Merycodus* were recovered, and relatively few limb elements were likewise found. A number of maxillaries and numerous rami with teeth occur. Fortunately, series of complete superior and inferior dentitions illustrate early stages of wear of deciduous teeth to advanced wear of permanent teeth with all intervening changes of crown pattern.

For the large number of individuals represented by rami, horn-cores and frontlets, there is a notable lack of axial and appendicular parts. In fact, the latter comprise only the distal end of a humerus; a hind leg lacking the femur; distal ends of three tibia; one complete and two proximal halves of metatarsals; parts of three calcani; a navicular-cuboid and a number of astragali and phalanges. In contrast, no less than sixty individuals are represented by rami, maxillaries, horn-cores and frontlets.

The frontlets with horn-cores and the detached horn-cores show diversity in size and form. Some of the differences are probably due to individual variation, age and sex. Pathogenic characters likewise may be exhibited. Certain constant characters which are present, when taken in association with dental structures, definitely exclude the Tonopah forms from specific identity with *Merycodus osborni*, *M. necatus*, *M. furcatus*, or with other known types.

A study of the cranial, dental and skeletal parts naturally segregates the collection into a large and a small group. The large group represents a species which may be described as follows:

Merycodus loxocerus n. sp.

Type specimen—No. 1301 C. I. T. Coll. Vert. Pale., right ramus.

Paratypes—No. 1268, left maxilla; Nos. 1298, 1256 and 719, rami, No. 1271, maxillary; and Nos. 696, 697, 698, 702, 705, and 707, horn-cores.

Merycodus loxocerus is characterized by the backward inclination of the horn-cores at an acute angle; lower molar teeth with sharply ridged anterior and posterior crescents; frequent occurrence of intercrescentic columnettes in $M\underline{1}$ and $M\underline{2}$, and by constancy in length of inferior dental series.

Merycodus loxocerus is represented in various stages of development from early youth to advanced age by the horn-cores and tooth series. The horn cores rise from the supra-orbital surface of the frontals, but do not possess the erect position seen in *M. necatus* and *M. furcatus*. In their position with relation to the orbit and in backward inclination, the horn-cores approximate more closely those in *M. osborni*.[1] They differ from those in *M. osborni* in having a practically straight beam and in possessing invariably two tines. Specimen No. 698 (Plate 1, figs. 2 and 2a) is an example of a young adult with slender beam, short anterior tine and relatively long posterior tine. Certain differences in proportion, due to individual variation or to age, occur in specimens No. 705 (Plate 2, figs. 1 and 1a) and No. 696 (Plate 3, figs. 1 and 1a). The former is not so slender and its front tine is less developed,

[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 20, art. 7, 101–129, 1904.

while in specimen 696 the tines are more fully grown, also their curvature toward the sagittal line is more pronounced. These specimens all possess burrs that occupy positions a short distance above the base of the beam. Specimen 697 (Plate 2, figs. 2 and 2a) is somewhat abnormal in growth and is probably a young individual in which the front tines have been suppressed. Many other specimens show incipiency of growth of anterior tines. All of the foregoing specimens probably represent young forms, and a cross-section of the proximal part of their beams is quite circular and the surface of the horn-cores is not deeply grooved by nutrient canals.

Specimens that are considered as belonging to adults of advanced age are notably more robust, although the beam and tines are relatively long. Specimens Nos. 702 to 707 (Plate 4, figs. 1, 1a and 2) and No. 1447 (Plate 1, figs. 1 and 1a) illustrate the larger size, deeper grooving of the horn-core surfaces and more oval cross-section through the beam. In the larger and older individuals, the proximal end of the beam is quite triangular in cross-section with apex forward.

The frontlets show the horn-cores to be parallel with one another and not widely spaced and that they arise from the posterior portion of the supra-orbital rim. The orbits are relatively large but not so prominent as in *M. osborni*. A most constant character in *Merycodus loxocerus* is the long slender beam with relatively short tines. *M. furcatus*[1] is distinguished by a like character, when compared with *M. necatus*, but the beams are not so slender relative to their height as in *Merycodus loxocerus*.

The uniformity of character in the large series of horn-cores, which range in size from small immature specimens to large apparently adult forms from Locality 172, indicates considerable specific stability in this respect.

Dentition—Merycodus loxocerus is represented by a large number of lower jaws, a right fragmental ramus, and full cheek-tooth dentition of a young adult, No. 1301. The crown pattern in the premolar and molar series is close to that in *M. necatus* and in other species of *Merycodus*. Premolar teeth with slightly worn crowns have the transverse crests and general pattern essentially similar in $P\bar{2}$ to $P\bar{4}$ inclusive.

The molar teeth in general are typical of the Antilocapridæ, but the crescentic pillars are more sharply ridged than in *M. necatus* or in *M. furcatus* (Plate 4, figs. 4 and 4a). Many of the specimens, as in No. 1301 (Plate 2, figs. 4, 4a and 4b) possess inter-crescentic columnettes in $M\bar{1}$ and $M\bar{2}$, and in the numerous paratypes this character is fairly constant. A comparable style between the anterior crescents of $M\bar{2}$ (Plate 2, figs. 4, 4a and 4b) may be present in a number of specimens. The third lobe in $M\bar{3}$ differs from that in *M. necatus*, U. C. No. 26781 (Plate 3, figs. 5, 5a and 5b), in being more lobate, not angular, and laterally compressed. In *M. furcatus*, U. C. No. 26795 (Plate 4, figs. 4, 4a and 4b), this character is more sharply emphasized. The lower dental series is fairly constant in anteroposterior diameter, with a maximum length of 46.8 mm. in an old adult specimen, No. 1259.

A left fragmentary maxillary, No. 1268 (Plate 2, figs. 3 and 3a) and No. 1267, a specimen with unworn teeth (Plate 3, figs. 3 and 3a), preserve the outer wall and retain the teeth $P\underline{3}$ to $M\underline{3}$ inclusive. The teeth do not differ significantly from those in *M. necatus* or in other *Merycodus* species. In another specimen, No. 1271 (Plate 1, figs. 3 and 3a), right $P\underline{2}$ is present and a complete tooth series is thus available. The buccal side of the alveolar wall develops an irregular surface, caused by prominence of the anterior roots of the cheek-teeth, a character not observed in *M. necatus* or in *M. furcatus*.

[1] E. L. Furlong, Univ. Calif. Publ. Bull. Geol., vol. 17, No. 4, 1927.

It is possibly an age character, for in another specimen, No. 1264, in which the complete deciduous dentition is present, the prominence of root wall is apparent only in the region of Dp $\underline{2}$ and Dp $\underline{4}$. The crown of M$\underline{3}$ is just appearing above the alveolar border in this specimen.

In adult individuals the tooth-row closely approximates 42.0 mm. in anteroposterior diameter (table 1).

Limb Elements—A hind leg lacking the femur (Plate 4, figs. 5, 5a, 5b and 5c), No. 1446, is referred to *Merycodus loxocerus*. Its slender proportions probably indicate a young adult individual.

The tibia, No. 1446, is long (Plate 4, fig. 5a); its proximal third is somewhat crushed, but the cnemial crest is high and the articular facets for the femur normal. The distal articular end is narrow with a high malleolar facet for the fibula and deep articular facets for the astragalus. In structure and proportion, the tarsal bones and phalanges are much like those in *M. necatus* and in *M. furcatus*.

Merycodus hookwayi n. sp.

Type specimen—No. 1257 C. I. T. Coll. Vert. Pale., ramus.

Paratypes—No. 710, maxillary; No. 712, ramus, and No. 1240, frontlet.

All specimens are from C. I. T. Locality 172.

Merycodus hookwayi is characterized by horn-cores much heavier than in *Merycodus loxocerus* or in *M. furcatus*. Their attitude, in relation to the orbit, is not so erect as in *M. necatus* or in *M. furcatus*, but the posterior inclination is less than in *Merycodus loxocerus*.

The inferior teeth are large with higher crowns, and the premolars are more simple in pattern than in *M. necatus* or in *Merycodus loxocerus*.

A frontlet with horn-cores, No. 1240 (Plate 5, figs. 1 and 1a), appears to present an anomalous type among the merycodonts from Locality 172. It is much heavier than the slender horn-cores described above. In comparison to the latter, this specimen is relatively broader across the frontals, as measured between the horn-cores. The beam is short and the tines likewise are relatively short. The posterior tine curves backward and toward the sagittal line. The horn-cores are more erect in attitude above the orbital rim than in *Merycodus loxocerus*, although inclined slightly posteriorly. Anteroposteriorly, in the region of bifurcation, the core is very broad. A large burr encircles the beam a short distance above its base.

Dentition—The following described jaws and teeth, differing as they do from those of *Merycodus loxocerus* in greater size and small numerical representation, are tentatively considered as representing the same type of merycodont known by the frontlet, No. 1240.

A right ramus, No. 1257 (Plate 5, figs. 3, 3a and 3b), is broken away at both ends; the tooth-row is complete with the exception of M$\overline{1}$; the ventral margin is present and shows decided convexity of surface from the posterior end of M$\overline{3}$ to the anterior end of P$\overline{2}$. The teeth indicate slight wear and are high crowned. P$\overline{2}$, P$\overline{3}$ and P$\overline{4}$ are characterized by high median transverse crests. The anterior crest in P$\overline{2}$ is low. Posteriorly, the crown is divided into two transverse crests. In P$\overline{3}$ the anterior crest is higher than in P$\overline{2}$, and in the latter a slight indentation is represented which becomes a deep infold in P$\overline{3}$, making the two transverse crests forward of the median apex. The back of the crown is divided into two transverse ridges, a deep pit separating the two. The enamel infolds from the lingual side in P$\overline{2}$ and P$\overline{3}$ are deep and extend beyond the fore and aft median line of the teeth, reaching downward to the cingulum.

The anterior crest in $P\bar{4}$ is not transverse in position, and terminates in a shallow notch on the lingual wall. A small lake lies anterior to the median crest, a character absent in *M. loxocerus*. In the latter species, however, a deep infold is present on the lingual wall of the tooth. The lingual wall in side view is like the anterior wall in the molar teeth; the anterior crest forming an anterior style. The median crest equals the anterior crest in molar teeth and is separated from the posterior part of the tooth by a deep infold of enamel.

The back of the crown is divided by a deep pit, with walls converging rapidly to the bottom, and with no infold on the inner side of the tooth. The posterior face of the tooth is slightly convex dorsoventrally. $M\bar{1}$ is absent in No. 1257. $M\bar{2}$ has anterior and posterior crescents sharply ridged from alveolus to crown. The anterior and posterior crests are flanked by a front and back style. $M\bar{3}$ has anterior crescents like the crescents in $M\bar{2}$. The anterior crest possesses two cuspules on its outer crown surface; the front style is strongly developed. The third lobe is not expanded and has a flat plane, posterior face. There are no intercrescentic cusps in $M\bar{2}$ or $M\bar{3}$. $M\bar{3}$ approximates in size and form the third molar of *M. altidens*[1] from the Upper Snake Creek beds. It differs in being smaller and more expanded anteroposteriorly; the anterior lobe of the tooth is relatively longer than the middle and posterior lobes, while in *M. altidens* the anterior lobe is relatively shorter.

The greatest diameter, $P\bar{2}$ to $M\bar{3}$ inclusive, is 56.3 mm. (table 1).

Superior dentition—Specimen No. 710 (Plate 5, figs. 2 and 2a), referred to *Merycodus hookwayi*, represents a fragmental left maxillary which includes part of the buccal wall and $P\underline{2}$ to $M\underline{2}$ inclusive. The teeth are those of an adult and show considerable wear. $P\underline{2}$, $P\underline{3}$ and $P\underline{4}$ differ little in detail from comparable teeth in other merycodonts, and this is true also for $M\underline{1}$ and $M\underline{2}$. The tooth-row is not so sinuous as in *M. necatus* or *M. furcatus*, but is straighter in its longitudinal alignment. The outer side of the maxillary is peculiar in the prominent expansion of surface covering the front roots of the cheek-teeth, thus leaving a depressed area between the front roots of the teeth at the alveolar border. Length of the dentition is approximately 51.2 mm. (table 1).

CORRELATION OF PARTS

Only a relatively small number of lower jaws and maxillaries can be definitely associated, due to the widely scattered distribution of the merycodont remains in the deposits. All of the frontlets and horn-cores were found separate from other cranial or facial parts. Segregation of the materials into two groups seems to answer best the representation of the merycodonts in the Tonopah fauna.

The largest assemblage of material representing *Merycodus loxocerus* considerably exceeds in number of specimens the collection on which is based the species *Merycodus hookwayi*. In the former group, individuals differing in age from youth to advanced adults are represented by specimens with deciduous to much worn permanent teeth. A representation of age characters is expressed also in stages of development of the horn-cores.

[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, art. 11, 198–206, 1924.

Merycodus hookwayi, known by remains of possibly more than three individuals, is distinct from *Merycodus loxocerus* in dental characters and in horn-core proportions. While the parts of the dentition and the horn-cores were not found associated, each individual specimen differs so widely in structural characters from its counterpart among specimens grouped under *M. loxocerus* as to suggest rather strongly that all relate to a single type, distinct from the latter.

With the exception of two relatively large astragali and a calcaneal fragment, possibly referable to *Merycodus hookwayi*, the limb elements in the collection are regarded as belonging to *Merycodus loxocerus*.

Among the horn-cores and frontlets known from the Tonopah locality, specimen No. 1240 (Plate 5, figs. 1 and 1a) is unique in its robustness and in the attitude of beam with reference to the skull, as well as in position of the tines. It is possible, owing to the similarity of dental characters among merycodont species, that certain specimens now grouped under *Merycodus loxocerus* actually belong to the former type.

An analysis of the measurements given in table 1 indicates a close uniformity of size for the tooth-row and for individual teeth among specimens referred to *Merycodus loxocerus*. The specimens measured are all adult forms, but the stage of wear represents individuals ranging in age from very mature to younger adult forms. The differences within the group are not very large. The limited material available of the species *M. necatus* and *M. furcatus*, in each instance representing an individual of well-advanced age, is intermediate in size between that of *Merycodus loxocerus* and that of *Merycodus hookwayi*.

DISTRIBUTION

Species of *Merycodus* form an integral part of the later Miocene and early Pliocene faunas from western North America and are known to have ranged during these stages of the Tertiary from the western Great Plains to and beyond the Great Basin Province.

M. necatus and *M. furcatus* with their variants are among the more commonly recognized forms. These are the species found in faunas of the Barstow Miocene, Ricardo Pliocene, Republican River Lower Pliocene, and Snake Creek Upper Miocene.

M. osborni[1] is apparently a more restricted species from the Pawnee Creek middle Miocene beds of Colorado. This species differs considerably from *M. necatus* and *M. furcatus* and approaches *Merycodus loxocerus* in position of the horn-cores and apparently also in size.

The upper Miocene merycodonts from near Tonopah may have been derived from a stock closely allied to *M. osborni* and may have occupied a similar life-zone, although of somewhat later age.

[1] W. D. Matthew, Amer. Mus. Nat. Hist., vol. 20, art. 7, 101–129, 1904.

TABLE 1—*Measurements (in millimeters)*

	Merycodus loxocerus n. sp.										*Merycodus hookwayi* n. sp.	
	No. 713	No. 717	No. 1247	No. 1248	No. 1249	No. 1250	No. 1252	No. 1259	No. 1261	No. 1298	No. 1307	No. 712	No. 1257
$P\frac{2}{2}$ to $M\frac{3}{3}$, inclusive, long diameter	44.0	43.0	45.4	45.3	.....	.....	45.2	46.8	44.0	45.4	44.8	59.6	56.8
$P\frac{2}{2}$, long diameter	4.5	.....	.....	4.4	5.0	.....	.....	4.9	4.8	.....	4.8	.....	6.0
$P\frac{3}{3}$, long diameter	5.2	6.6	5.7	6.3	6.3	5.8	6.6	6.1	6.4	6.0	6.0	.....	6.9
$P\frac{4}{4}$, long diameter	6.6	6.7	6.6	6.6	7.0	7.5	5.7	7.3	7.2	6.9	6.9	a7.8	8.9
$M\frac{1}{1}$, long diameter	6.9	7.0	7.5	7.6	7.8	7.0	7.8	8.1	7.7	7.2	7.4	9.2	.....
$M\frac{2}{2}$, long diameter	7.8	7.7	8.4	8.2	9.0	8.2	8.0	9.4	8.1	8.0	8.3	10.4	11.0
$M\frac{3}{3}$, long diameter	12.5	12.6	12.8	12.0	.....	11.1	12.0	12.3	11.5	12.0	11.8	15.0	14.0

	Merycodus loxocerus n. sp.		*Merycodus hookwayi* n. sp.		*M. necatus* U. C. No. 26781	*M. furcatus* U. C. No. 26745
	No. 1266	No. 1271	No. 710			
$P\frac{2}{2}$ to $M\frac{3}{3}$, inclusive, long diameter	41.8	40.2	a51.0	$P\frac{2}{2}$ to $M\frac{3}{3}$, inclusive, long diameter	51.4	50.7
$P\frac{2}{2}$, long diameter	6.4	6.0	7.4	$P\frac{2}{2}$, long diameter	5.5	4.9
$P\frac{3}{3}$, long diameter	.....	.....	7.4	$P\frac{3}{3}$, long diameter	5.9	5.4
$P\frac{4}{4}$, long diameter	6.1	.....	6.8	$P\frac{4}{4}$, long diameter	6.6	6.8
$M\frac{1}{1}$, long diameter	7.2	6.6	8.5	$M\frac{1}{1}$, long diameter	7.6	8.3
$M\frac{2}{2}$, long diameter	8.2	8.3	10.0	$M\frac{2}{2}$, long diameter	8.8	10.0
$M\frac{3}{3}$, long diameter	8.4	8.8	.....	$M\frac{3}{3}$, long diameter	16.0	15.2

a, approximate.

CONCLUSIONS

New species of *Merycodus*, not heretofore reported, occur in beds of the Esmeralda formation of upper Miocene age near Tonopah, Nevada. *Merycodus loxocerus* is represented by many individuals and is associated with the more sparsely occurring species, *Merycodus hookwayi*. Remains of both forms and of associated mammalian types were uncovered in a relatively small area, where they had evidently accumulated in a small lake or watering hole.

Merycodus loxocerus exhibits considerable uniformity of tooth structure and of the structure of the horn-cores in the large series of specimens available. This species approximates *M. osborni* more closely than it does other known species in pattern of the teeth and in the position of the horn-cores.

If the lower jaw specimens, Nos. 1257, 712, pertain to the same species as the frontlet, No. 1240, the species *Merycodus hookwayi*, established on the basis of frontlet as type, may be distinguished from *M. loxocerus* not only in shape and proportions of horn-cores, but also by its marked difference in size and in pattern of the premolar teeth. The higher crowned teeth and peculiar enamel pattern of $P\bar{4}$ in *M. hookwayi* may warrant a generic recognition of this form, when more material becomes available.

PLATE 1

Merycodus loxocerus n. sp.

FIG. 1—Front view of frontlet of mature individual; 1a, lateral view; No. 1447; x ½.

FIG. 2—Front view of frontlet showing closely spaced and parallel position of horn-cores; figure 2a, lateral view showing long beam, relatively short tines and sharp postorbital inclination of horn-cores; No. 698; x ½.

FIG. 3—Right superior dentition; figure 3a, left superior dentition; No. 1271; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.

Merycodus loxocerus n. sp.

PLATE 2

Merycodus loxocerus n. sp.

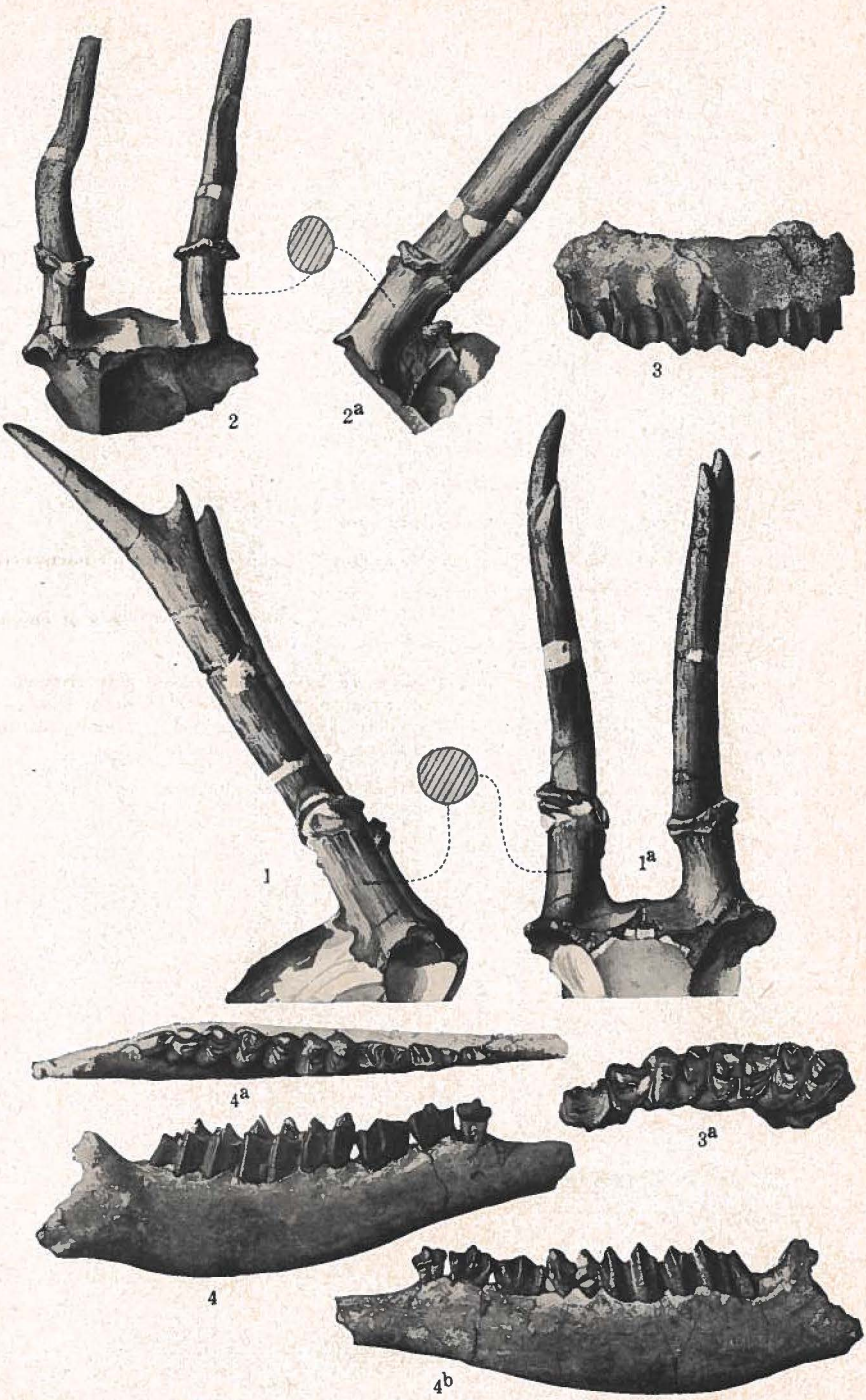
FIG. 1—Side view of frontlet; figure 1a, anterior view; No. 705; x ½.

FIG. 2—Front view of frontlet; figure 2a, side view showing abnormal growth of horn-cores in young individual; No. 697; x ½.

FIG. 3—Side view of left maxillary with depressed areas in wall between roots of cheek-teeth; figure 3a, occlusal view; No. 1268; x 1.

FIG. 4—Buccal view of left ramus illustrating sharp crescentic pillars, intercrescentic columnettes; figure 4a, occlusal view showing transverse crests in premolars and lobate form in posterior crescent of M3; figure 4b, lingual aspect of ramus showing deep infolds in walls of premolars; No. 1301; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.



Merycodus loxocerus n. sp.

Plate 3

Merycodus loxocerus n. sp.

Figs. 1, 1a—Front and lateral views of frontlet with horn-cores; No. 696; x ½.

Fig. 2—Fragment of right horn-core showing superficial character of burr; No. 687; x ½.

Figs. 3, 3a—Lateral and occlusal views of maxillary with slightly worn P3 to M3; No. 1267; x 1.

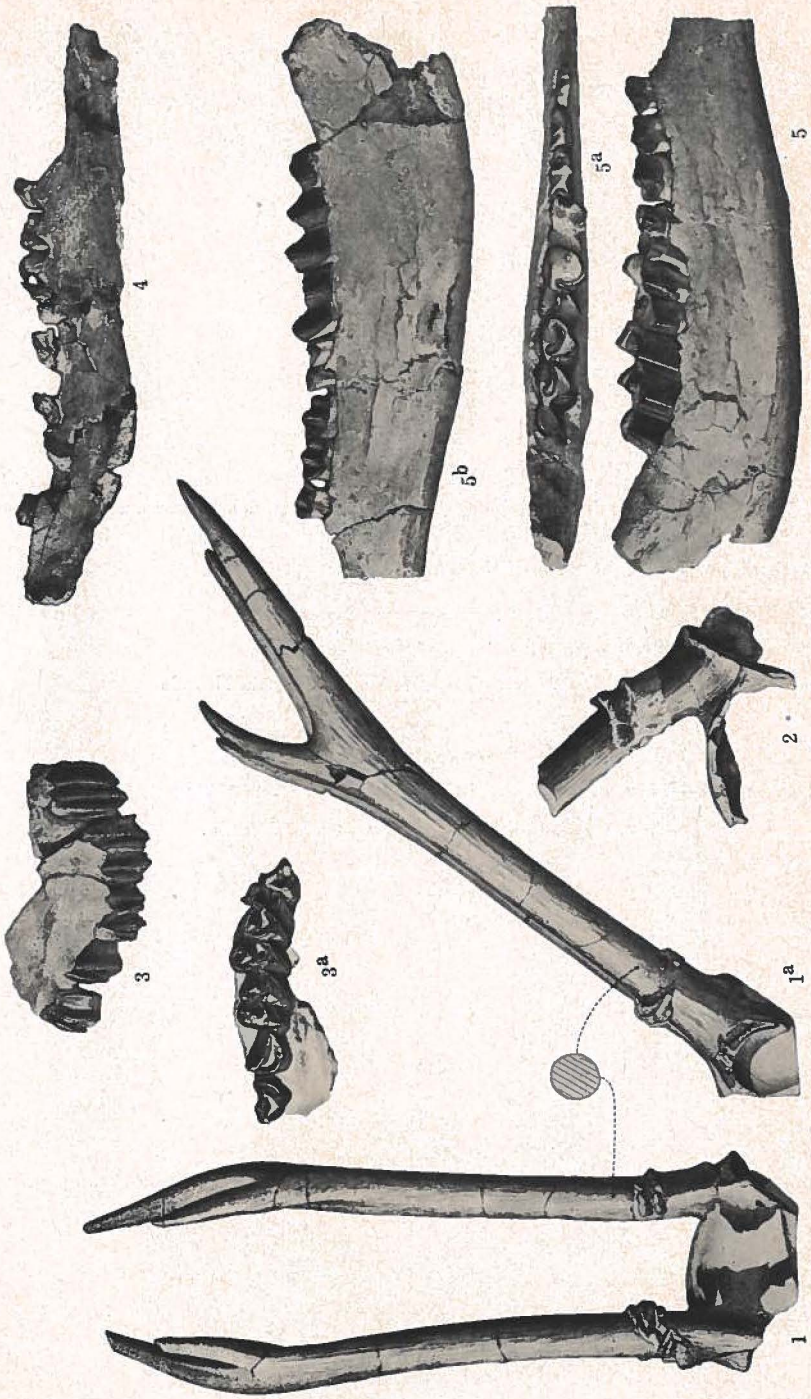
Fig. 4—Lingual view of ramus of an old individual; No. 1256; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.

Merycodus necatus Leidy

Figs. 5, 5a, 5b—Views of ramus to compare with specimen of *Merycodus loxocerus* shown on Plate 2, figures 4, 4a, and 4b; No. 26781; x 1.

Univ. Calif. Coll. Barstow Miocene, California.



Merycodus loxocerus n. sp. and *Merycodus necatus* Leidy

PLATE 4

Merycodus loxocerus n. sp.

FIGS. 1, 1a—Horn-cores of adult individual showing long beam, deep sinuses, and oval cross-sections; No. 707; x ½.

FIG. 2—Distal portion of horn-core; No. 702; x ½.

FIG. 3—Buccal view of right ramus; No. 1298; x 1.

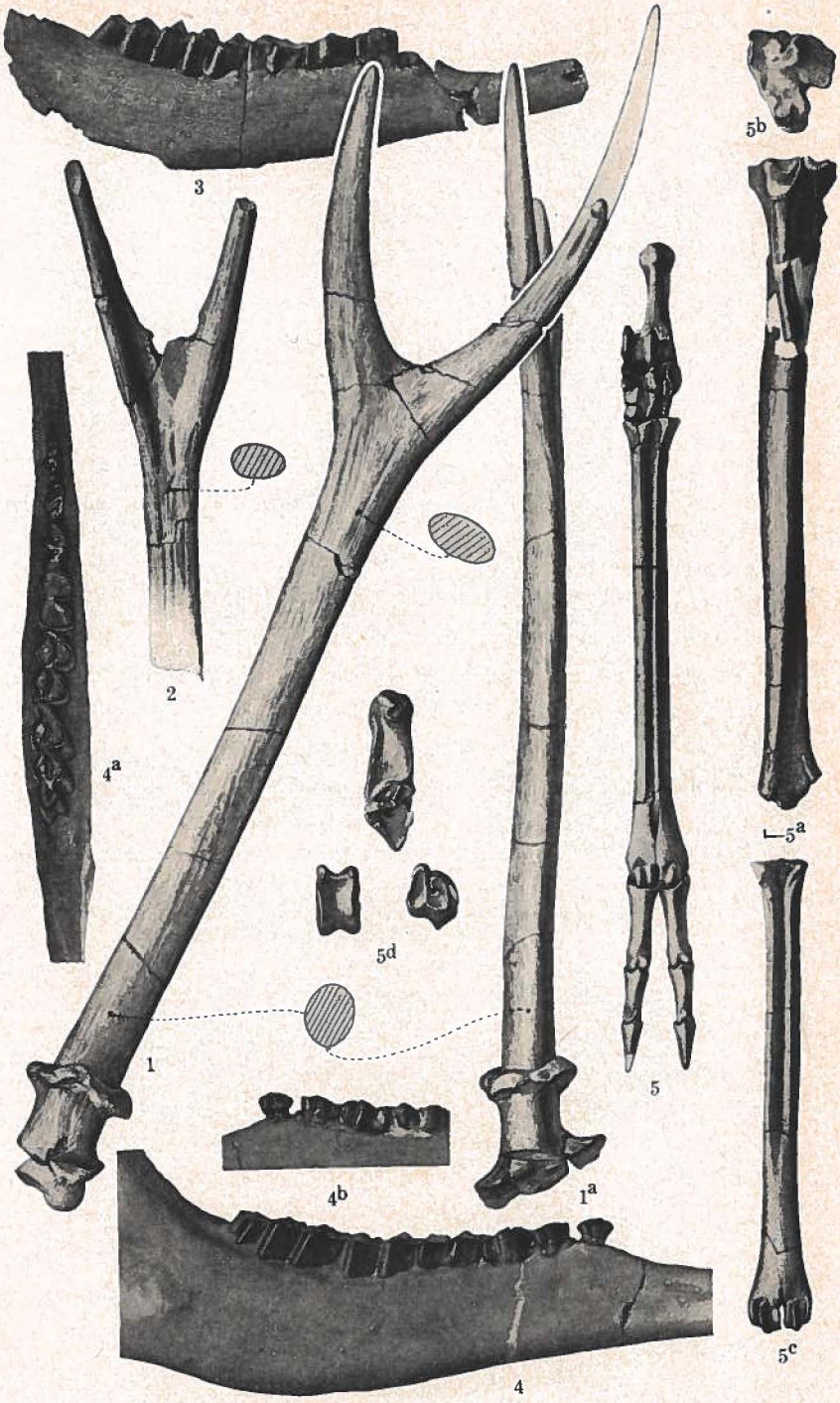
FIGS. 5 to 5c—Elements of the hind leg; No. 1446; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.

Merycodus furcatus Leidy

FIGS. 4, 4a and 4b—Views of ramus and inferior dentition; No. 26795; x 1.

Univ. Calif. Coll. Ricardo Pliocene, California.



Merycodus loxocerus n. sp. and *Merycodus furcatus* Leidy

PLATE 5

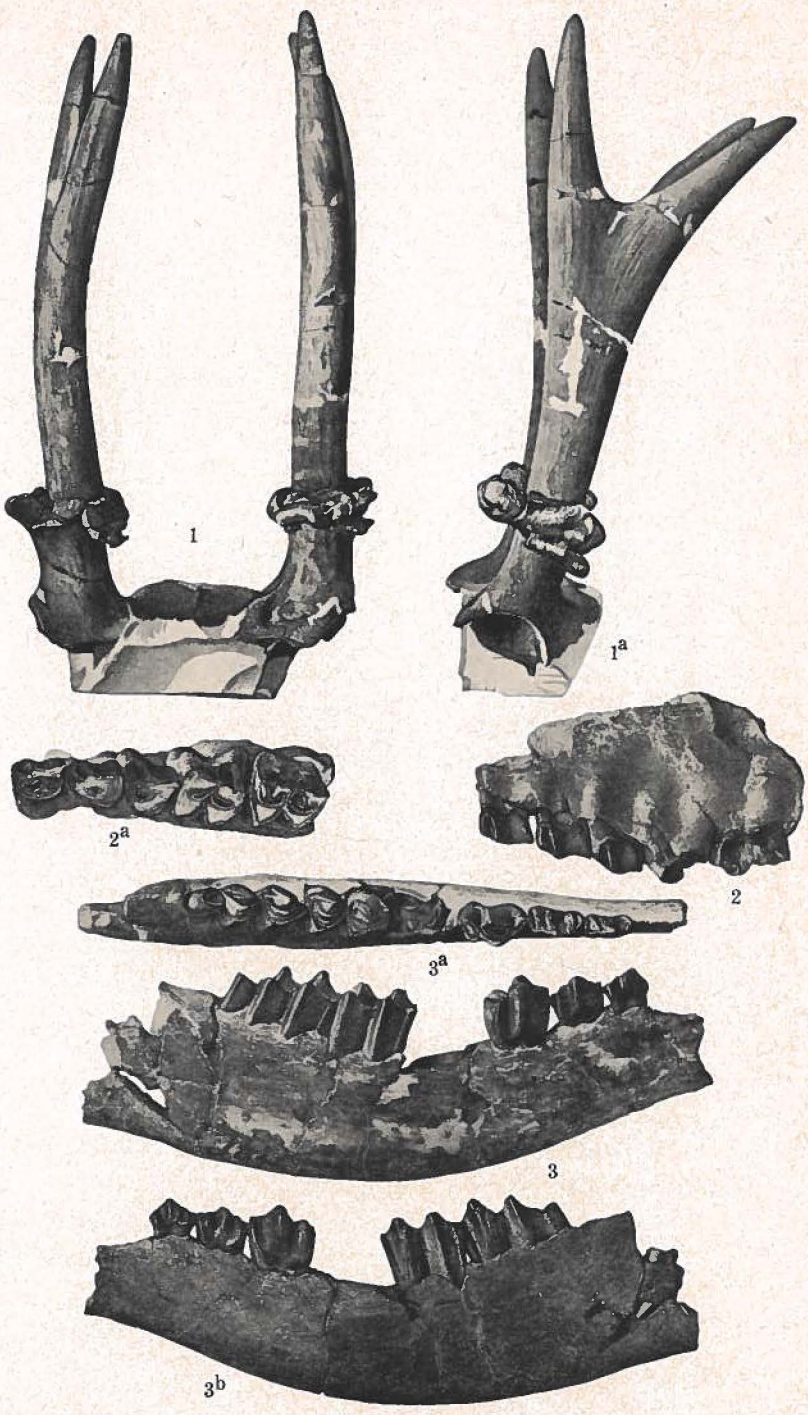
Merycodus hookwayi n. sp.

FIGS. 1, 1a—Front and lateral views of horn-cores; No. 1240; x ½.

FIGS. 2, 2a—Lateral and inferior views of maxillary fragment; No. 710; x 1.

FIGS. 3, 3a and 3b—Lateral and occlusal views of ramus; No. 1257; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.



Merycodus hookwayi n. sp.